Adaptive morphology in the Black and Slatey Egrets *Egretta ardesiaca* and *Egretta vinaceigula*, and relationships within the genus *Egretta* (Aves: Ardeidae)

By

MICHAEL P. STUART IRWIN

National Museum of Rhodesia, Bulawayo

Introduction

The Black Egret *Egretta ardesiaca* feeds, often socially in shallow water, arching the wings forward to form a very characteristic umbrella-like canopy and letting the tips trail in the water. The diet seems to consist principally of fish, but no detailed investigations of food preferences appears ever to have been undertaken and the various statements in the literature are by no means absolutely clear. Rand (1936: 331) records twelve fish measuring between 15 to 30 mm in the stomach and throat of a bird. B. G. Donnelly (in litt.) also informs me that a Black Egret collected on Lake Kariba on 7 May 1971 contained the following food items: 2 *Tilapia mortimeri* of 50 and 56 mm in length, 1 *Tilapia rendalli* of 50 mm, 1 indet. *Tilapia* of 50 mm, 1 indet. *Tilapia* of 54 mm and the remains of four other *Tilapia*. Total weight 15.5 g (B.G.D.). Young *Tilapia* occupy the shallow shorelines during the day and are therefore prone to heron predation. On the other hand Murton (1971: 98) states that prawns and aquatic insects feature much in the diet, but does not quote an authority. Du Plessis (1963: 111—112) has shown how while so fishing, the resulting elimination of reflections will greatly improve visibility underwater. Such a canopy also cuts off the light from above the surface and apparently enables the bird to see much more effectively because it is looking out of the shade into the light. It may also have the effect of obscuring from the fish any sudden movement when the bird strikes. Broekhuysen & Broekhuysen (1961: 184—185) have also suggested that the shade formed by the canopy may induce small fish to seek the shadow so cast in the water. These last authors, as well as Farkas (1962: 20), have pointed out that this type of behaviour would appear to be innate, exhibiting all the characteristics of a ritualised repetitive behaviour pattern which has not however lost its original meaning. Cooper (1970: 212, 214) gives further support to this general view. These arguments all point to such behaviour as being ancient and long established.

The all black plumage might also be considered as assisting materially in this fishing technique. Murton (1971: 97—99) has argued the adaptive significance of polymorphism in the Ardeidae and by inference the significance of colour generally in relation to feeding ecology. Recher (1972: 552—555) has, however, contested Murton's arguments concluding that it is difficult to make any correlation between the way in which a heron hunts and the colour of the bird. Nevertheless it seems inescapable that the all black plumage of *E. ardesiaca* would be the most effective means of creating an area of shade.

The Slatey Egret *Egretta vinaceigula* is much less well known and has, in the past, with one or two exceptions, usually been regarded as a colour phase of the Black Egret. But, as shown by Benson, Brooke and Irwin (1971: 131—133), it differs from that species in a number of morphological characters and must be regarded as a distinct species. In support of these arguments, Vernon (1971: 157—159) was able to demonstrate that it also differed from the Black Egret in not spreading its wings when feeding, being more similar in habits to the Little Egret *Egretta garzetta,* feeding solitarily, either by standing motionless or by stalking and then stabbing at prey. The Slatey Egret was not however seen chasing prey or stirring the water with its feet as the Little Egret is stated to do. It is also believed to feed principally on fish.

The rather belated recognition of *E. vinaceigula* as a valid species partly reflected the fact that only three specimens, all being males, were known to exist in the Museums of the World, and, until the note by Vernon (1971), nothing was known of its habits or ecology. Consequently further specimen material was highly desirable in order to understand more fully the limits of variation within this species and to gain a greater understanding of its general morphology. This has been materially assisted since two further specimens, including the unknown female, have become available.

Mr. John E. du Pont III, of Easton, Maryland, while on a hunting expedition in Botswana, obtained a pair of Slatey Egrets at Xugana, 19° 04′ S., 23° 06′ E. near the Khwae River in the north-eastern part of the Okavango swamps. Through the kindness of Mr. du Pont I have been able to examine this additional material which has in turn prompted this further investigation of the relationships of these and other egrets.

The characters of *E. vinaceigula* and *E. ardesiaca*

These two specimens of *E. vinaceigula* agree completely with the one already in Bulawayo, having the throat vinous coloured, a pale base to the lower mandible, and white bases to the shafts of the primaries. The underparts are also uniform with the praepectoral plumes slatey grey and the abdomen and flanks a uniform black. Of the five specimens now known, only one of the two birds in the British Museum (Natural History), at Tring differs significantly in having the breast and abdomen washed with vinous

with the centre of the lower throat and some of the long praepectoral plumes also vinous. Table I gives the measurements of this new material.

Table I. Standard measurements

Egretta vinaceigula	♂	♀
wing	236	226
culmen (from nostril slit)	60	56
tarsus	82	76

These figures are in close agreement with those given by Benson et al. (1971) for the three previously known specimens and confirm the consistently smaller size of this species when compared with *E. ardesiaca*.

It can now be shown that there are other consistent morphological differences that distinguish the two species. The proportions of the foot are for example diagnostic, the somewhat shorter on average tarsus in *E. vinaceigula* is accompanied by a more gracile foot of different proportions, the various elements being wholly smaller. This is shown by the following measurements for the middle and hind toes and claw, between it and *E. ardesiaca*.

Table II. Comparative measurements of the foot

E. ardesiaca	7 ♂	5 ♀
middle toe (with claw)	61—68 (65.4)	62—68 (64.4)
hind toe (with claw)	37—39 (38.0)	36—40 (38.4)
hind claw	14—17 (16.0)	14—17 (15.4)

E. vinaceigula *	2 ♂	♀
middle toe (with claw)	56,56	56
hind toe (with claw)	30,34	31
hind claw	14.5,15	14

* includes the specimen already in Bulawayo.

The leg and foot colour of *E. vinaceigula* would never seem to have been properly recorded in life, although it has been apparent from skins that the legs were probably a dull yellowish green (not black), as in *E. ardesiaca*. While the colours in these relatively freshly collected specimens were not noted, the legs would clearly appear to have been concolorous greenish or

olivaceous, with the soles only of the feet a pale yellowish olive, again in contrast to the wholly yellow or orange feet of *E. ardesiaca*. C. J. Vernon (in litt.) states that the legs are possibly yellowish in life, but the feet are certainly so, but was unable to provide more precise information. As *E. garzetta* also possesses yellow feet the question may be posed as to the possible purpose of such a colour combination and whether or not it has any practical significance.

Yet other and important characters occur that reflect very clearly the known differences in their feeding ecology. Among herons the fishing technique of *E. ardesiaca* is perhaps unique. In fact the question ought perhaps be asked, is not so much how *E. vinaceigula* differs from *E. ardesiaca*, but the reverse, and how, in the light of its specialised habits, has *E. ardesiaca* become modified morphologically. An examination of the structure and development of the wing in the two species reveals this immediately.

In *E. ardesiaca* the primaries are consistently broader and more sharply emarginated near the tip and with the outer web also broader. The secondaries are very well developed and broad with the shafts becoming soft and degenerate on the outer half of their length and reach to the tips of the primaries. The scapulars too, are equally broad and almost confluent with the trailing edge of the secondaries. The under wing coverts are also broad and the supporting axillaries well developed and more elongated, almost half the length of the secondaries. In contrast all these elements in *E. vinaceigula* are less well developed with primaries and secondaries narrower, the latter having the shafts fully reinforced throughout their length, while the narrower scapulars fall considerably short of the secondaries.

All the main elements in the wing of *E. ardesiaca* therefore appear to have become modified so that it may form a complete and effective umbrella when stretched forward. This has been achieved principally through the unusual broadening and lengthening of the secondaries and in the development of the scapulars. On the other hand the corresponding wing elements in *E. vinaceigula* show no such specialisation and are much more normal.

Other specific differences are present that have no immediately apparent adaptive significance. The plumes on the hind neck in *E. vinaceigula* are much less numerous, narrower and more filamentous, in the undescribed female reaching to a length of only about 55 mm whereas in the male the longest plumes exceed 100 mm. On the foreneck the plumes are similar to those of *E. ardesiaca*, but are more strongly developed in the male. Further differences occur in the back plumes, those of *E. vinaceigula* projecting beyond the tip of the tail in the male whereas they fall short of the tail in *E. ardesiaca*. Those of *E. vinaceigula* are in turn narrower and more attenuated, and always with a conspicuous twist to the lanceolate tips that is lacking in *E. ardesiaca*. It might well be suggested that if two such similarly coloured species were to nest together in a mixed heronry, differences in the ornamental plumes might be important in courtship and territorial behaviour.

Distributional aspects

Both *E. ardesiaca* and *E. vinaceigula* are endemic to the Ethiopian region, are fully sympatric, and presumably evolved there. Of the two, *E. ardesiaca* is the more widespread occurring over the greater part of Africa where conditions are suitable and on the island of Madagascar, and although never very numerous, it may be locally quite common. In contrast *E. vinaceigula* would seem to have a very restricted distribution and in respect of numbers and range, may well be the rarest of all the world's herons. So far as is known it would seem to be confined in its distribution to the Chobe and Okavango swamps in Botswana and in the adjacent Caprivi, perhaps breeding throughout this region. As it also occurs on the ecologically suitable Kafue Flats in Zambia it may also breed there too, as well as in parts of south-eastern Angola. Its occurrence at Potchefstroom, where it was first discovered in the last century may only have been accidental. Vernon (1971) quotes evidence that it is absent from the Chobe River during the rains, so, as with all large waterbirds, individuals may at times turn up well outside of their usual range. Vernon (1971) has suggested that it occupies a niche which is only created in marshes and flood plains, more especially where the water levels are falling. Such conditions are common to many river systems in Africa, so it is difficult to explain why it should have such a restricted range.

It may be that through some unknown factor it is naturally declining towards extinction and everything points to its being a relict species. There is therefore an urgent need that we should learn more about it in life.

Other relationships

While *E. ardesiaca* diverges significantly in such strictly adaptive features as the modification of the wing elements, it would nevertheless seem that these two species are very closely related in terms of their basic external morphology and plumage. Indeed, it would appear that they are closer to each other than to any other species of the genus *Egretta*. As they may occur together in the same habitat and must have done so over a great period of time, and therefore be to some extent in competition with each other, it is all the more surprising that the differences separating them are not in fact greater. Again, the apparently innate, even ritualised feeding behaviour of *E. ardesiaca* must presumably have been long established.

By comparison, the three equally sympatric all white species, *E. garzetta*, *E. intermedia* and *E. alba*, while supposedly closely related are all more different between themselves than are either *E. ardesiaca* and *E. vinaceigula*. All three in the breeding season assume profusely aigretted plumes on the back, but whereas *E. garzetta* has in addition two elongated plumes emerging from the nape, no such adornment is present in the other two species which also lack the elongated and lanceolate feathers on the lower neck and chest that are present in *E. garzetta*. In general too, the conformation of the wing in all three varies. In *E. garzetta* the secondaries are very

much shorter than the primaries while the scapulars are proportionately longer, almost as long in fact as the longest primaries. *E. intermedia* differs in that the secondaries just fall short of the longest primaries, with the scapular feathers falling short of the secondaries. In *E. alba* the secondaries exceed the length of, and overlap the primaries but with the scapular plumes proportionately similar to those of *E. intermedia*. In these three forms the wing elements are relatively broader in proportion to the size of the individual species than in the case of *E. vinaceigula*, but do not quite approach that found in *E. ardesiaca*.

It is not proposed to discuss here the adaptive significance of any of the above differences, but merely to illustrate that they appear proportionately greater to those found between *E. ardesiaca* and *E. vinaceigula*. A more detailed investigation of such differences between these and other species of herons might nevertheless prove worthwhile.

Phylogenetic lines in the genus *Egretta*

While Benson et al. (1971) followed most recent authors in not recognising the genus *Hydranassa*, as was advocated by Bock (1956) in his generic review of the Ardeidae, it would appear that such a concept has some taxonomic reality. A good deal of evidence can now be brought forward in support of the argument that those egrets generally with lanceolate plumes, are, as was argued by Bock, the more primitive and have preceded the evolution of the advanced species of *Egretta* which possess the highly evolved and typically aigretted form of ornamental plumes. This argument can be initially based on Bock's assumption, that the aigretted condition arose through an intermediate stage as represented by the development of the elongated lanceolate plumes which typify the species he placed in *Hydranassa* and to which he accordingly referred *E. ardesiaca*.

Apart from *E. ardesiaca* (of which *E. vinaceigula* was then regarded as a colour phase), Bock placed four other species in *Hydranassa*. These were *E. caerulea*, *E. tricolor* and *E. rufescens* of the New World and *E. picata* with a restricted range from Celebes eastwards to New Guinea and northern Australia. The position of the two groups on the major continental land masses can now be viewed in perspective.

Of the New World hydranassine egrets, reference to the distribution maps in Palmer (1962) illustrates that only *E. caerulea* is in any sense of really widespread breeding distribution there, both *E. tricolor* and *E. rufescens* being confined to a rather limited portion of coastal southern North, Central, and northern South America. The only other representatives of *Egretta* in the Americas are the almost cosmopolitan *E. alba*, and the endemic *E. thula*. Both are very wide ranging there and have a breeding range far exceeding that of any member of the *Hydranassa* group (see distribution maps in Palmer, 1962). Curry-Lindahl (1971: 53—70) goes as far as regarding *E. thula* as conspecific with the Old World *E. garzetta*, or at least forming a twin species with it, from which it was derived. Bock (1956)

has however, previously contested this suggestion. But if this concept is accepted, both it and *E. alba* can be considered virtually world wide in distribution. *E. alba* it may be noted is tentatively placed in the genus *Ardea* by Curry-Lindahl, an action that has received some support from other authors. It would therefore seem that both these members of the advanced group of egrets must be considered as having colonised the New World only relatively recently.

The specialised mode of feeding adopted by *E. ardesiaca* may enable it to avoid competition with such rather similarly-sized species as *E. garzetta* and *E. intermedia,* as well as the very much larger *E. alba.* Murton (1971) especially remarked that *E. ardesiaca* seemed to be a highly evolved and specialised egret and that its plumage characters seemed to indicate a close affinity with the ancestors of *Egretta.* This is certainly consistent with it being part of a more ancient lineage. The present relict status of *E. vinaceigula* may in turn be due to both interspecific competition and the restricted nature of the niche it would seem to occupy. On the other hand in parts of the east coast of Africa *E. ardesiaca* apparently competes successfully with *E. gularis* which it replaces locally (Murton, 1971). But nowhere in the Ethiopian region can even *E. ardesiaca* be regarded as a dominant water bird demonstrating yet again the relative unimportance of the hydranassine members of the Ethiopian Ardeidae.

The position with *E. picata* in Australasia would appear again to be similar with everything pointing to its being of relict distribution. Such a situation is to be expected if it is assumed that these two major phylogenetic lines within the genus *Egretta* are in some sort of basic competition wherever they occur, with the hydranassine species in decline particularly in the Old World tropics where the presently more successful group of egrets presumably arose, and where indeed all of the species or their geographical representatives occur at the present time.

With these facts in mind, strong arguments can be put forward for the recognition of *Hydranassa* as a valid genus representing an older, but clear evolutionary level within the Ardeine herons. In advocating this, it must be remembered that the all-embracing concept of the broadly based genus *Egretta,* sensu White (1965), Curry-Lindahl (1971), is by no means universally accepted. Wetmore et al. (1957), Palmer (1962) and de Schauensee (1966) still retain the three New World hydranassine egrets in the monotypic genera *Dichromanassa (rufescens), Hydranassa (tricolor)* and *Florida (caerulea),* although de Schauensee at least regarded them all as perhaps best placed in *Egretta.*

This also is the decision adopted here. The lack of hard and fast taxonomic characters throughout the group as a whole mitigates against their being broken up into smaller generic units. Despite this, the hydranassine section within *Egretta* are probably monophyletic and should be grouped together, as should likewise the more advanced group of aigretted species to which they gave rise. This treatment generally remains very similar to that of Curry-Lindahl (1971) who has provided the most recent review.

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Summary

A study of two further specimens of the rare Slatey Egret *Egretta vinaceigula* reveals new morphological characters, particularly in the structure of the wing and the proportions of the feet, that distinguish it from the related Black Egret *Egretta ardesiaca*.

The Black Egret is in turn shown to have the main elements of the wing specially adapted through the broadening of the primaries and the broadening and lengthening of the secondaries and scapulars, the whole structure being an adaptation towards the formation of a more effective umbrella-like canopy when fishing.

Relationships within the genus *Egretta* are also discussed and it is concluded that the various species with lanceolate ornamental plumes that are sometimes associated together in the genus *Hydranassa*, are indeed more closely related to each other than to any of the more advanced species with more specialised aigretted ornamental plumes.

The hydranassine egrets are also considered to be a declining group, probably through competition with the more advanced forms.

Both groups of species are however placed in the genus *Egretta* due to the difficulty in establishing diagnostic characters other than the possession of specialized ornamental plumes. The concept of the genus *Hydranassa* nevertheless appears to have some taxonomic reality.

Zusammenfassung

Die Untersuchung von zwei weiteren Stücken des seltenen Braunkehlreihers, *Egretta vinaceigula*, brachte neue morphologische Kennzeichen ans Licht, die ihn von dem verwandten Glockenreiher, *Egretta ardesiaca*, vor allem in der Struktur der Flügel und in der Proportion der Füße unterscheiden.

Für die letztere Art konnte gezeigt werden, daß die hauptsächlichen Eigenarten ihrer Flügel — verbreiterte Handschwingen und lange und verbreiterte Armschwingen und Schulterfittiche — eine Anpassung an das Verhalten darstellen, im Schatten einer mit den Flügeln gebildeten „Glocke" oder eines Schirms zu fischen.

Die verwandtschaftlichen Beziehungen innerhalb der Gattung *Egretta* werden diskutiert, wobei der Verfasser zu dem Schluß kommt, daß die zuweilen als Gattung *Hydranassa* vereinigten Arten mit lanzettförmigen Schmuckfedern in der Tat untereinander näher verwandt sind als mit den abgeleiteten Arten mit zerschlissenen Schmuckfedern.

Die Reiher der *Hydranassa*-Gruppe scheinen im Rückgang befindlich zu sein, für den vermutlich die Konkurrenz der abgeleiteten Arten die Ursache ist.

Obwohl *Hydranassa* als eigene Gruppe zu erkennen ist, möchte der Verfasser sie nicht als eigene Gattung von *Egretta* trennen, da es schwer fallen dürfte, andere diagnostische Merkmale als die Form der Schmuckfedern aufzufinden.

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Address of the author: Michael P. Stuart Irwin, National Museum, P. O. Box 240, Bulawayo, Rhodesia.